

Observations on Hawaiian Species of *Wikstroemia* (Angiospermae: Thymelaeaceae)¹

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Wikstroemia (Thymelaeaceae) is a genus of tropical and subtropical shrubs or trees, widely distributed in southeast Asia to Malaysia, north-east Australia, and the Pacific islands (Ryukyu, Marianas, Caroline, Hawaiian, Society, Marquesas, Tonga, Fiji, Norfolk, and New Caledonia). The Hawaiian species are known by the name *Akia* or *Akea*.

The genus *Wikstroemia* was described by Endlicher in 1833 from Norfolk Island. The type species is *Wikstroemia australis*. Many new species have since been described. Some species were further divided and some segregates were accorded specific rank. Ohwi (1965) mentioned 50 species, while Ding Hou (1960) estimated 70 species in the genus. However, a total of at least 161 species names have been recognized.

Meisner (1857) divided the genus into two sections: *Diplomorpha* (albuminous seed, ebaccate, nonsucculent fruit); and, *Euwikstroemia* (= *Wikstroemia*) (exalbuminous seed, baccate and succulent fruit). Ding Hou (1960) reports that in the Malaysian species of section *Wikstroemia* there is morphological variation not only within a single species, but also in the flowers of one specimen. He also quotes a similar observation, by Peterson, for African Thymelaeaceae. The Hawaiian species of *Wikstroemia* all belong to the widely distributed section *Wikstroemia* that Ding Hou recognizes as a subgenus. In this subgenus there are 6 species in the Philippines, 3 in New Guinea, 1 in Fiji, 5 in Borneo (Ding Hou, 1960), 1 in Samoa, 7 in Japan (Ohwi, 1965), and 22 in Hawaii. This indicates a remarkable speciation of *Wikstroemia* in the Hawaiian Islands.

The Hawaiian *Wikstroemia* have been studied by Gray (1865) and Hillebrand (1888), and

most thoroughly by Skottsberg (1936, 1944a, 1964), yet the identification of the Hawaiian species is extremely difficult. The published morphological descriptions are often inconsistent and ambiguous. Every study has resulted in the addition of more species. Skottsberg recognized a total of 22 species (Table 1). Of these 22 species, 14 are restricted to one island: 4 to Oahu, 2 to Kauai, 3 to Maui, 1 to Molokai, 1 to Lanai, and 3 to Hawaii. The remaining 8 species are found on more than one island.

Extreme diversity in the general morphological expression, habit, and habitat preference occurs in the Hawaiian species of *Wikstroemia*. They occur on well-drained to poorly drained soils and also on arid habitats of lava flows. This habitat diversity can be found within a single species. The genus occurs from sea level to 1800 meters, under moisture regimes varying from 0.5 to 5 meters per year. In native vegetation, the plants often occur associated with *Scaevola*, *Metrosideros*, *Diospyros*, etc.

Duration of flowering is 3 to 5 months, generally from May through September, but this varies in different species and in different localities. Populations obtain ingress to new territory probably through the dispersal of the drupaceous fruits by birds.

The habit of the Hawaiian species is highly variable. Plants are procumbent to erect; low shrubs to small trees. This variation can be found within a single species and even in the same population.

Above all, the morphological features of the leaves, flowers, and fruits are most variable. The leaves in this genus vary from 2.5 to 16 cm in length and 0.7 to 4 cm in width. Variation in the texture of the leaves has been noticed within a single species. The length of the inflorescence rachis varies from less than 1 mm long, or nearly capitate, to 150 mm long and distinctly racemose. Hillebrand (1888) cites the extensive variability in the flowers of this genus. We have observed that the flowers of a single species may

¹ Abstracted from a thesis submitted by the senior author in partial fulfillment of the requirements for the degree of Master of Science at the Graduate School, University of Hawaii. Manuscript received April 30, 1968.

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TABLE 1
THE HAWAIIAN SPECIES OF *Wikstroemia*

SPECIES	REFERENCES
<i>W. sandwicensis</i> *	Meisner (1857)
<i>W. elongata</i>	Gray (1865)
<i>W. buxifolia</i>	Gray (1865)
<i>W. uva-ursi</i> *	Gray (1865)
<i>W. phillyreifolia</i> *	Gray (1865)
<i>W. hanalei</i>	Wawra (1875)
<i>W. bicornuta</i>	Hillebrand (1888)
<i>W. villosa</i>	Hillebrand (1888)
<i>W. oahuensis</i> *	Rock (1913)
<i>W. furcata</i> *	Rock (1913)
<i>W. recurva</i> *	Skottsberg (1936)
<i>W. haleakalensis</i>	Skottsberg (1936)
<i>W. leptantha</i> *	Skottsberg (1936)
<i>W. caumii</i>	Skottsberg (1936)
<i>W. pulcherrima</i> *	Skottsberg (1936)
<i>W. sellingii</i> *	Skottsberg (1944a)
<i>W. skottsbergiana</i>	Sparre (1964)
<i>W. isae</i> *	Skottsberg (1964)
<i>W. vacciniifolia</i> *	Skottsberg (1964)
<i>W. forbesii</i> *	Skottsberg (1964)
<i>W. eugenoides</i> *	Skottsberg (1964)
<i>W. lanaiensis</i>	Skottsberg (1964)

* Chromosome counts obtained in this study.

be unisexual or bisexual within the same population (*Wikstroemia oahuensis*) or in different populations (*W. phillyreifolia*). The length of the floral tube was found to be shorter in the female flowers, longer in the male flowers of some species. The fruit shape ranges from ellipsoid to fusiform to globose and varies in color from yellow to orange to red.

From this information it is evident that the use of morphological features in the demarcation of species in this genus often results in uncertain determinations.

In recent years cytological data have been used successfully as important criteria in taxonomic work. The chromosome number often shows a high degree of stability within a species and often correlates with the natural grouping of species. More important, chromosome studies often reveal critical information on evolutionary dynamics, and this information aids in the interpretation of difficult genera such as *Wikstroemia*.

Skottsberg (1953) has reported chromosome counts for two Hawaiian species: *Wikstroemia uva-ursi* (from Kauai, $2n = 18$, and Maui, $2n = 72$); and *W. pulcherrima* (from Hawaii, $2n = 36$). An apomictic triploid has been re-

ported by Fagerlind (1940) in the widely distributed Asian species, *W. indica*.

MATERIALS AND METHODS

Collections of *Wikstroemia* were made from the islands of Kauai, Maui, Hawaii, Molokai, and Oahu. Populations sampled are given in Table 2.

Cytological Studies

All chromosome studies were made from the microsporocytes. The young flower buds were collected and fixed (by placing in chloroform-ethanol-acetic acid 4:3:1) for 24 to 48 hours, then transferred to 70 per cent ethanol-water and stored in the refrigerator until used.

Microsporocytes were removed from the anthers by dissection and smeared in acetocarmine. The slides were stored in the refrigerator (12 to 24 hours) until stained to the desired intensity.

OBSERVATIONS AND RESULTS

Chromosome counts of 27 populations were determined (Fig. 1), these representing the 13 species listed in Table 2. These counts show that all populations, with the exception of the one of *Wikstroemia pulcherrima*, are diploid with 9 pairs of chromosomes. The one population of *W. pulcherrima* has the chromosome complement of 18 pairs (Fig. 2), confirming the earlier somatic count on this species by Skottsberg (1953). This population is characterized by aberrant chromosome pairing (see multivalents in metaphase I chromosomes in Fig. 2), and by the unequal segregation of chromosomes in anaphase I. The plant studied had a relatively low fertility, the percentage of "good" pollen being 55 in 1,000 grains observed. These observations suggest that this is an autotetraploid.

Our studies of flower morphology indicate that floral dimorphism is present in all 13 species studied, confirming earlier observations by Skottsberg (1936, 1944a) and Carlquist (1966). However, we have found bisexual as well as unisexual flowers in three species: *Wikstroemia phillyreifolia* (Gupta 132, 313, and 314), *W. oahuensis* (Gupta 268), and *W. furcata* var. *furcata* (Gillett 2104, 2105). Our

TABLE 2
Wikstroemia CHROMOSOME NUMBERS, COLLECTION DATA, AND SPECIES

SPECIMEN NUMBER	LOCATION AND ELEVATION	SPECIES	CHROMOSOME NUMBER
Gupta 136-2	Wiliwilinui Ridge, Koolau Range, Oahu (600 m)	<i>W. oahuensis</i>	n = 9
Gupta 142	Aiea Loop Trail, Koolau Range, Oahu (400 m)	<i>W. oahuensis</i>	n = 9
Gupta 160	Kipapa Gulch, Koolau Range, Oahu (520 m)	<i>W. oahuensis</i>	n = 9
Gupta 178	Waahila Ridge, Koolau Range, Oahu (50 m)	<i>W. oahuensis</i>	n = 9
Gupta 130	Bishop Museum, Oahu (50 m)	<i>W. uva-ursi</i>	n = 9
Gupta 139	Kawai-iki Ditch Trail, Koolau Range, Oahu (400 m)	<i>W. sellingsii</i>	n = 9
Gupta 141	Aiea Loop Trail, Koolau Range, Oahu (400 m)	<i>W. sellingsii</i>	n = 9
Gupta 148	Halemano Intake No. 1, Koolau Range, Oahu (400 m)	<i>W. isae</i>	n = 9
Gillett 2104	Halemanu, Kokee, Kauai (1200 m)	<i>W. furcata</i> var. <i>furcata</i>	n = 9
Gillett 2105	Halemanu, Kokee, Kauai (1200 m)	<i>W. furcata</i> var. <i>furcata</i>	n = 9
Gupta 149	Haena-Kalalau Trail, Haena, Kauai (80 m)	<i>W. furcata</i> var. <i>palustris</i>	n = 9
Gupta 167	Haena-Kalalau Trail, Haena, Kauai (80 m)	<i>W. furcata</i> var. <i>palustris</i>	n = 9
Gupta 170	Haena-Kalalau Trail, Haena, Kauai (80 m)	<i>W. furcata</i> var. <i>palustris</i>	n = 9
Gupta 174	East of Kokee, Kauai (1200 m)	<i>W. furcata</i> var. <i>palustris</i>	n = 9
Gupta 155	Kawailoa Summit Trail, Koolau Range, Oahu (1200 m)	<i>W. recurva</i>	n = 9
Gupta 176	Waahila Ridge, Koolau Range, Oahu (50 m)	<i>W. eugenoides</i>	n = 9
Gupta 200	Puu Kanehoa Trail, Waianae Range, Oahu (700 m)	<i>W. leptantha</i>	n = 9
Gupta 223	Road to Mt. Kaala, Waianae Range, Oahu (800 m)	<i>W. leptantha</i>	n = 9
Gupta 304	South slope of Haleakala above Kanaio, E. Maui (600 m)	<i>W. vacciniifolia</i>	n = 9
Gillett 2005	Lahainaluna, Maui (900 m)	<i>W. vacciniifolia</i>	n = 9
Gupta 311	Near Black Sand Beach, Chain of Craters Road, Hawaii (60 m)	<i>W. sandwicensis</i>	n = 9
Gillett 2061	45 miles south of Kona, Hawaii (600 m)	<i>W. sandwicensis</i>	n = 9
Gupta 314	Near Black Sand Beach, Chain of Craters Road, Hawaii (60 m)	<i>W. phillyreifolia</i>	n = 9
Gupta 315	15 miles northeast of Volcano House, Hawaii (750 m)	<i>W. phillyreifolia</i>	n = 9
Gupta 318	Pahala; 51 miles from Hilo, Hawaii (400 m)	<i>W. phillyreifolia</i>	n = 9
Gillett 2109	Above Kaunakakai, Molokai (350 m)	<i>W. forbesii</i>	n = 9
Gupta 322	Parker Ranch, near Puu Waawaa, Hawaii (800 m)	<i>W. pulcherrima</i>	n = 18
Gupta 324	Parker Ranch, near Puu Waawaa, Hawaii (800 m)	<i>W. pulcherrima</i>	n = 18



FIG. 1. Drawing of meiosis in microsporocytes of Hawaiian *Wikstroemia*. A, *W. oahuensis* (Gupta 142); B, *W. sandwicensis* (Gillett 2061); C, *W. leptantha* (Gupta 200); D, *W. recurva* (Gupta 155); E, *W. furcata* var. *palustris* (Gupta 149); F, *W. selligii* (Gupta 139); G, *W. isae* (Gupta 148); H, *W. eugenoides* (Gupta 176); I, *W. uva-ursi* (Gupta 130); J, *W. phillyreifolia* (Gupta 314); K, *W. vacciniifolia* (Gillett 2005); L, *W. furcata* var. *furcata* (Gillett 2104); M, *W. forbesii* (Gillett 2109).



FIG. 2. Drawing of meiosis in microsporocytes of *Wikstroemia pulcherrima*. Left: metaphase chromosomes showing 7 quadrivalents (on the right) and 4 bivalents (on the left). Right: anaphase I showing segregation of 18 chromosomes (above) and 18 chromosomes (below).

observations show that monoecism, dioecism, and polygamodioecism are present in the Hawaiian species of *Wikstroemia*.

DISCUSSION

A limited cytological study of *Wikstroemia* in Hawaii shows that 12 of the 13 species investigated are characterized by the diploid chromosome number of $n = 9$, the chromosomes being of similar size. Thus there is a close cytological affinity. The one exception to this number is *W. pulcherrima* with the tetraploid complement of $n = 18$. The latter species is restricted to a limited area on the island of Hawaii. It shows a close morphological affinity with *W. phillyreifolia*, also restricted to that island, but more widely distributed. The two species resemble each other in all respects except that *W. pulcherrima* has larger flowers, fruit, and leaves. The stigma of *W. pulcherrima* is more capitate than that of *W. phillyreifolia*. Thus it seems possible, from cytological evidence (the presence of quadrivalents, aberrant segregation, low pollen fertility) and morphological evidence, that *W. pulcherrima* could be an autopolyploid race of *W. phillyreifolia*.

Our observations show that the predominant breeding system in these species is a relatively

high level of outcrossing. All species studied are characterized by floral dimorphism, and various levels of dioecism, monoecism, and polygamodioecism prevail. These conditions facilitate a strong expression of outbreeding. The presence of bisexual flowers in three species shows that outbreeding may not be an exclusive system, and that a measure of inbreeding may take place. The perfect flowers studied have the stigma close to the anthers, so that self-pollination is possible. There is no evidence of dichogamy in these flowers, so that barring self-incompatibility, a most unlikely possibility, there is every opportunity for inbreeding. Lastly, there is strong cytological evidence of inbreeding in the putative autotetraploid, *Wikstroemia pulcherrima*.

The great diversity in the Hawaiian species of *Wikstroemia* may be due to hybridization between species. Skottsberg (1936) suspected hybridization in this genus. He cited specimens that are similar to what Gray described as *W. buxifolia* but indicated that he suspected them to be hybrids of *W. phillyreifolia* and *W. sandwicensis*. We have observed *W. sellinii* and *W. leptantha* growing together along the road to Mt. Kaala, Oahu. Also, we have seen *W. isae* and *W. sellinii* in the same population near Halemano Intake No. 2, Koolau Range, Oahu. These species all have the same chromosome number, and they flower at the same time over a considerable period of time, so that the possibility of interspecific hybridizations should be given serious consideration.

ACKNOWLEDGMENTS

The support of the Watumull Foundation, the Hawaiian Botanical Gardens Foundation, and the National Science Foundation is gratefully acknowledged. Appreciation is extended to Dr. Bo Peterson, Botanical Museum, University of Göteborg, for his review of the manuscript.

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